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# Clonal Variation in Apical Dominance of Triplochiton scleroxylon K. Schum. in Response to Decapitation

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### Summary

Clonal trials with the West African hardwood *Triplochiton scleroxylon*, K. Schum. have indicated a positive relationship between stem size (height and diameter) and branching frequency (mean no. of branches per m of mainstem). As part of a programme of vegetative propagation and clonal selection, the present study with young plants examined clonal variation in apical dominance, the process which determines branching frequency. Young potted plants of five clones were decapitated by removing the apex and uppermost node. The plants were partially defoliated, leaving 4 to 6 leaves at the apical nodes. These plants were grown in a glasshouse at 25 °C to 30 °C under experimental conditions testing:- (i) two rates of fertilizer application (4.0% and 0.04% liquid feed, NPK = 23:19.5:16); (ii) three rates of water application, ranging from field capacity to severe water stress (watering with 250 ml either every day, every three days or every 12 days); and (iii) two daylengths (10 h and 19.5 h). The length and number of lateral shoots formed on these decapitated plants were measured weekly to determine the percentage bud activity. In the first four weeks after decapitation, percentage bud activity increased (Sprouting Phase) and, thereafter, it declined as dominance was re-imposed (Dominance Phase). Peak bud activity at week 4 was greatest with the higher rate of nutrient application under the daily and 3-day watering regimes, but was unaffected by daylength. During the Dominance Phase, bud activity remained high at the higher rate of nutrient application, under the 3 and 12-day watering regimes and under long days. The relative performance of different clones was consistent in all treatments. Of the three clones used in all experiments, clones 8038 and 8049 had similarly high activity (rank one or two) and clone 8053 displayed less activity. However, inconsistencies in clonal ranking occurred under the lowest rate of watering. Responses to decapitation can thus be used as a robust indicator of genetic variation in apical dominance, provided care is taken: (i) to avoid extreme environmental conditions; and (ii) to maintain uniformity in the morphological (height, no. of leaves etc.) and physiological state (eg water and nutrient status) of the plants and their growing environment (especially light).

Key words: apical dominance, correlative inhibition, clonal variation, branching, decapitation, screening test, tree improvement, *Triplochiton scleroxylon*.

### Introduction

The development of techniques for clonal propagation of several West African hardwoods has been the basis of a tree improvement programme involving the selection of superior genotypes (Leakey *et al.*, 1982; Leakey, 1986). The gene pool of many species in West Africa is dysgenic, as a result of selective logging. The approach taken has been to vegetatively propagate young trees and to make selections based on their field performance in clonal trials (Howland and Bowen, 1977). Although genetic gains are made faster by this approach than by traditional forms of tree improvement, it is still laborious, expensive and slow. It would be desirable therefore to find a clonal trait in young plants that could be correlated with later yield in replicated trials.

What are suitable physiological criteria for this purpose and to what extent can any juvenile trait be used to predict adult performance? In a previous paper (Ladipo *et* al., 1984), we have shown that the $CO_2$ exchange rates of young plants can be used to predict the rank order of timber yield of *Triplochiton scleroxilon* K. Schum. clones in a trial plantation. The commercial quality of a tree,

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however, depends not only on its accumulated biomass, but also on stem straightness and freedom from undesirable branching characteristics. In earlier studies, it was noted that fast growing *T. scleroxylon* clones often had a low branching frequency (mean no. of mainstem branches $m^{-1}$) (Ladipo *et al.*, 1983), while stockplants cropped regularly for cuttings varied considerably in the numbers of branches produced following decapitation (Leakey, 1983). Consequently ,it was postulated that much of the variation in branching habit may arise from genetically-determined differences in apical dominance (sensu stricto, Brown *et al.*, 1967; Leakey, 1985). Furthermore, it was suggested that these genetic differences may be detected on juvenile plants following removal of the terminal shoot. (Leakey and Ladipo, 1987). Such decapitation, it is suggested, quantifies inherent differences in apical dominance, as the number of lateral shoots can easily be determined following the release of the axillary buds from the influence of apical dominance.

In this paper, we examine in young plants the response of several clones to decapitation, with a view to developing a screening test for use in the field. It has already been demonstrated that the responses of different clones to decapitation may be modified by environmental and physiological variables (Ladipo, 1981; Leakey and Longman, 1986). Consequently, the primary aim of the work described here was to determine whether differences between clones are consistent when grown under different conditions, particularly with regard to variables which are known to affect apical dominance such as nutrient and water availability (McIntyre, 1976 and 1977). In subsequent papers, we present (i) evidence that decapitation of young trees under nursery conditions in Nigeria were comparable with those from glasshouse studies in Britain (Ladipo *et al.*, in prep. a) and that except under extreme environments ranking between clones was consistent, and (ii) correlations between the outcome of standardised screening test and the stem form of a number of clones from a replicated field trial in Nigeria (Ladipo *et al.*, 1991).

## Materials, Methods and Experimental Details

### *Plant material and culture*

Seed of *T. scleroxylon* were collected from different locations in Nigeria (*Table 1*), germinated and the seedlings propagated vegetatively in Edinburgh (Leakey *et al.*, 1982). Four clones were used in this study. After rooting, the plants were transferred over a few months from 8 cm to 13 cm and then to 18 cm diameter pots containing potting compost (7:3:1 mixture of peat, sand and loam enriched with 4.2 g $kg^{-1}$ 'Enmag', 2.6 g $kg^{-1}$ 'John Innes' base and 0,3 g $kg^{-1}$ of trace elements )and grown in a glasshouse at 25 °C to 30 °C. Once a week the daily watering was supplement with liquid fertilizer (1% Solufeed-ICI,23N : 19.5 P : 16 K). Except where otherwise stated, the daylength was 19.5 h, with natural daylight supplemented by mercury vapour lamps (400 W), as necessary, such that irradiance at plant level was in the range 150 to 1500 $\mu mol\ m^{-2}\ s^{-1}$. Plants were arranged in randomized blocks, with 7 to 10 replicates of each of 3 to 4 clones per treatment.

### *General procedures*

At the start of each experiment, unbranched trees about 0.6 m to 1.0 m tall were decapitated by removing the apex and uppermost node. The plants were made more uniform by removing the lower leaves, so retaining either four or six leaves per plant. Depending on the number of treatments, plants were arranged in twos (Expts. 1 and 3) or threes (Expt. 2) of uniform size, and then one of each set was allocated at random to each treatment. The shorter plants were raised so that the tops of all plants were at the same level. Following decapitation, the lengths of allateral shoots were measured each week over a period of 9 to 12 weeks, to determine percentage of bud activity (% of buds/shoots per plant elongating by more than 2 mm per week). Standard errors for percentage bud activity were analysed by Bailey's (1959) procedures for binomially distributed data.

### *Effects of nutrients*

Thirty two days prior to decapitation, 60 plants (20 x 3 clones) were repotted from 13 cm to 18 cm diameter pots. The normal fertilizer regime (1% Solufeed) was replaced by two new fertilizer treatments, 250 ml of 0.04% and 4.0% Solufeed, given twice per week. Following decapitation, leaflets from all but the top six nodes were removed.

### *Effects of watering regime*

One hundred and twenty plants (30 x 4 clones) in 4.7 l pots were reduced to 6 leaves and allocated to one of three watering regimes ,in which plants were given 250 ml of water either daily ,every 3 days or every 12 days. These treatments represent a range from field capacity to severe water stress (*Table 2*). To reduce water loss from the soil surface, each pot standing in its own saucer was covered by a polythene bag tied around the plant stem but split at the base to allow water uptake from the saucer. Some aeration was allowed by two 15mm diameter holes on the upper surface of the bags. Twelve days after the start of the watering treatments, the plants were decapitated and two leaves (from Nodes 3 and 4 from the top) were removed to determine leaf water potential using a pressure bomb. At the same time, the angle of the leaf at the pulvinus was measured. At the end of the experiment (week 12) the laminar area of 4 new leaves from the uppermost lateral shoot were measured using a Lambda leaf area meter (model 3100).

### *Effects of daylength*

Eighty plants (16 x 5 clones) were decapitated after one week's acclimatization to two daylengths (10 h and 19.5 h) in the glasshouse. The long daylength was natural daylight extended from 10 h to 19.5 h by artificial lighting (400 W mercury vapour lamps) of c. 150 $\mu mol\ m^{-2}\ s^{-1}$ at plant level. There were 6 h of artificial light before and 3.5 h after the period of daylight. Black polythene was used to screen the short-day plants from other light sources. At the end of the experiment, leaf areas were assessed using a Lambda leaf area meter.

### *Conceptual basis for interpretation*

Following Leakey and Longman (1986), the response ~~to~~ decapitation was considered as having two phases. In the first (the Sprouting Phase), lateral buds become active over a period of 3 to 4 weeks. Thereaster (the Dominance Phase) lower shoots become progressively inhibited by the upper ones. It is assumed that clones with strong apical dominance release few lateral shoots following decapitation, while those with weak apical dominance sprout more freely.

*Table 1.* — Origins of the *T. scleroxylon* clones used in this study.

| Clone No. | Location | Latitude N | Longitude E | Rainfall (mm) |
|---|---|---|---|---|
| 8035 | Ilugun | 7° - 21' | 3° - 39' | 1300-1500 |
| 8038 | Ilugun | 7° - 21' | 3° - 39' | " |
| 8047 | Igbo-Ora | 7° - 27' | 5° - 37' | 1000-1300 |
| 8049 | Igbo-Ora | 7° - 27' | 5° - 37' | " |
| 8053 | Iwo to Ibadan road | 7° - 38' | 4° - 37' | 1300-1500 |

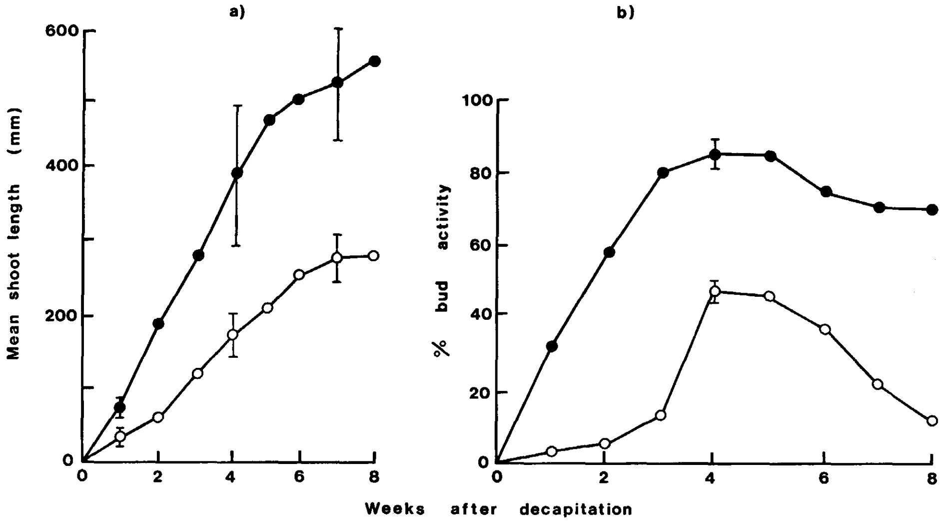

*Figure 1.* — Effects of nutrient applications (● = 4% 'Solufeed', 0 = 0.04% 'Solufeed') on (a) mean length of top four lateral shoots tnd (b) bud activity (percentage of buds growing more than 2 mm week$^{-1}$) of decapitated plants of *T. scleroxylon*. Vertical bars = ± SE.

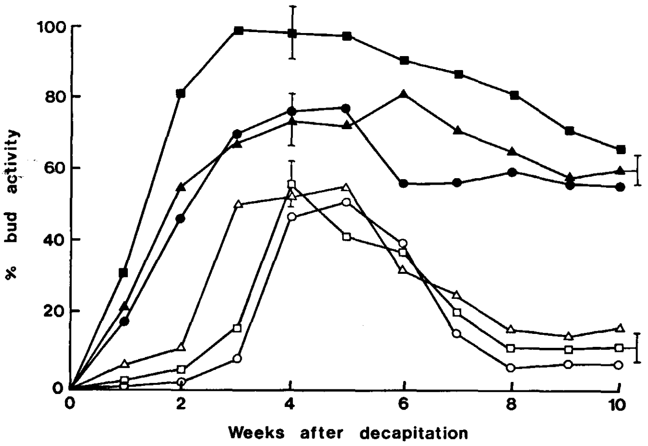

*Figure 2.* — Effects of high (solid symbols) and low (open symbols) applications of nutrients (Solufeed tt 4.0% and 0.04%) on the percentage of actively growing shoots on decapitated plants of three *T. scleroxylon* clones (▲△ = 8038, ●□ = 8049, ●○ = 8053).

## Results

### *Effects of nutrients*

The top four shoots was significantly longer on plants receiving the higher rate of nutrient application from one week after decapitation (*Fig. 1a*), as was percentage of bud activity (*Fig. 1b*). Peak bud activity was reached in both treatments four weeks after decapitation. Thereafter, dominance by the uppermost shoot was reimposed at the low rate of nutrient application, while with the high rate of nutrients 66% of shoots were still growing at week 10. Although clones responded differently to treatment, the differences between them within treatment at week 4 were statistically significant only at the higher rate of nutrient application (*Fig. 2*). Clone 8049 had more active shoots than clones 8038 and 8053.

### *Effects of watering regime*

At the end of the first 12-day watering cycle, mean leaf water potential and leaf angle were strongly correlated ($r = 0.96$, $P = 0.05$) with leaf water potential reaching —3.8 MPa under the low watering regime (*Table 2*).

Only the 12-day watering cycle affected bud activity during the first four weeks (Sprouting Phase) reducing it sharply in week 3. Thereafter, both the 3 and 12 day cycles delayed the re-establishment of dominance (*Fig. 3*). Bud activity fluctuated considerably during the Dominance Phase in response to the 12-day watering regime. The successive decreases in water availability between treatments were also associated with reduced mean shoot length and leaf area (*Table 3*).

Clones 8038 and 8049 responded similarly to decapitation in all treatments, with a consistently high level of bud activity, while clone 8047 had a significantly lower level of bud activity (*Fig. 4*). Clone 8053 was intermediate, although under the 12-day watering regime, it shared with clone 8038 a peak level of bud activity at week 4 which was significantly higher than the other two clones (*Fig. 4c*). This extreme treatment did, therefore, result in some

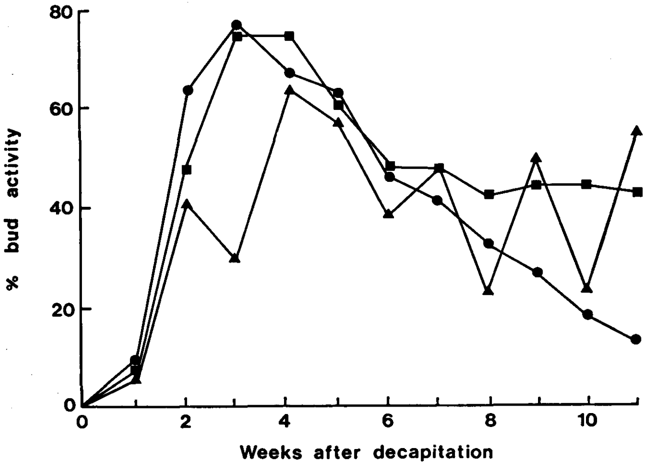

*Figure 3.* — Effects of there watering regimes (250 ml applied ● = daily, ■ = every 3 days, ▲ = every 12 days) on bud activity of decapitated plants of *T. scleroxylon.*

*Table 3.* — Effects of three watering regimes (250 ml applied every 1, 3 or 12 days) on mean shoot length and leaf area (week 12) lateral shots formed on decapitated plants of *T. scleroxylon* (means of 5 clones).

| Watering cycle | Mean shoot length (mm) | Leaf area ($cm^2$) |
|---|---|---|
| Daily | 263 ± 8 | 357 ± 9 |
| Every 3 days | 199 ± 7 | 296 ± 26 |
| Every 12 days | 69 ± 7 | 259 ± 17 |

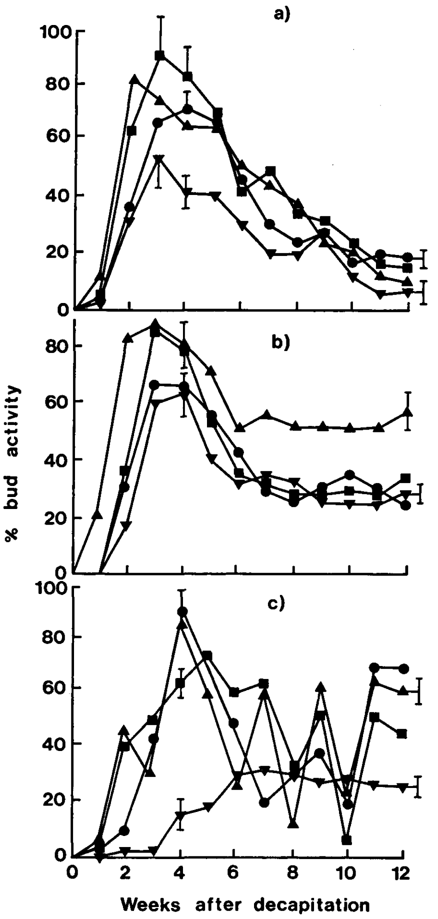

*Figure 4.* — Effects of three 250 ml watering regimes (a) daily; (b) every 3 days and (c) every 12 days on bud activity (percentage of buds growing more than 2 mm week$^{-1}$) of decapitated plants of four *T. scleroxylon* clones (▲ = 8038, ▼ = 8047, ■ = 8049, ● = 8053).

inconsistency in clonal response. On the other hand, clone 8047, although consistent in terms of clonal ranking, was also unusual in that sprouting was delayed and its leaves were significantly smaller than those of other clones (*Fig. 5*). These responses to low water availability in clone 8047 resulted in substainable bud activity ,in contrast to the fluctuations of other clones, arising from watering every third or twelfth day. Clonal differences in mean shoot length were positively correlated with bud activity at 4 weeks ($r = 0.50$, $p = 0.05$) and mean leaf area ($r = 0.72 : P < 0.01$) at 12 weeks.

### *Effects of daylength*

There was no appreciable effect of daylength on the peak level of bud activity at week 4, but long days delayed the re-establishment of dominance (*Fig. 6*).

Clones maintained their ranking in both treatments, with clones 8038 and 8049 having the greatest and clone 8047 the least bud activity (*Figs. 7a* and *b*). A fifth clone, 8035, not included in the other experiments of the present study, had a level of bud activity intermediate between clones 8053 and 8047. Substantial differences between daylength treatments were also found on mean shoot length (SD = 180 mm: LD = 375 mm), mean leaf area (SD = 80.4 $cm^2$: LD = 132.2 $cm^2$) and mean number of leavers produced (SD = 27.6: LD = 49.6).

## Discussion

Earlier studies identified that physiological and environmental conditions that affect the activity of lateral buds of *T.scleroxylon* released from apical dominance by decapitation, both under glasshouse (Leakey and Longman, 1986) and nursery conditions (Ladipo *et al.*, in prep. a and 1991). It was also shown that clones varied in their response to decapitation, some having inherently greater bud activity than others. Consequently, it has been postulated that clones vary genetically in the 'strength' of their apical dominance and that this may be a useful criterion for clonal selection (Leakey and Longman, 1986). Field trials

Table 2. — Effects after 12 days of three watering regimes (250 ml applied every 1, 3 or 12 days) on the mean leaf water potential and leaf angle in decapitated plants of *T. scleroxylon* (means of 5 clones).

| Watering cycle | Leaf water potential (MPa) | Leaf angle | Wilting |
|---|---|---|---|
| Daily | -0.07 | 90° | - |
| Every 3 days | -1.9 | 45° | day 3 |
| Every 12 days | -3.8 | 18° | day 3 |

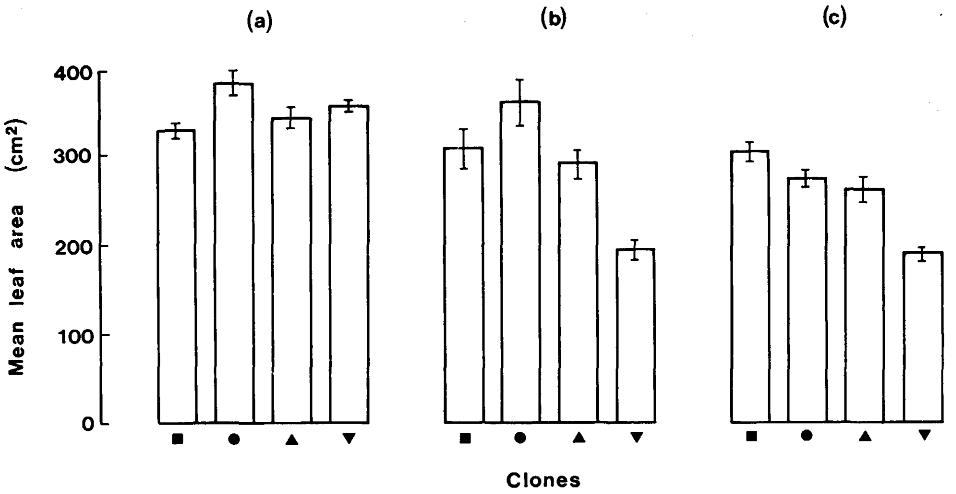

*Figure 5.* — Effects of three 250 ml watering regimes (a) daily; (b) every 3 days and (c) every 12 days, on mean leaf size produced on the top 4 lateral shoots of decapitated plants of 4 *T. scleroxylon* clones (▲ =8038, ▼ = 8047, ■ = 8049 and ● = 8053), by week 12.

in Nigeria have demonstrated that clones with a low branching frequency tend towards greater stem productivity per tree (Leakey and Ladipo, 1987). A technique to predict genetic variation in branching frequency while plants are still in the nursery could therefore be a means of screening seedlings and clonal lines for desirable genotypes, prior to field testing.

*Responses to treatment*

The present study, like the previous ones, demonstrated the sensitivity of apical dominance, as expressed by decapitation, to environmental factors. Furthermore, it has confirmed, that high levels of nutrition and long daylength delay the establishment of dominance. In the present study, unlike that of Leakey and Longman (1986), daylength was confounded by different levels of total radiation. Nevertheless, the responses to decapitation under different daylengths were similar to plants grown in glasshouses or controlled-environment cabinets.

The present study also indicated the importance of avoiding water stress when determining clonal variation in bud activity. Clone 8047 grew slowly and produced the smallest leaves of all clones used, but made continous growth over the course of the experiment. It therefore showed its ability to balance its rate of shoot growth and leaf area to water availability. As this clone comes from a relatively dry area, the ability to tolerate infrequent watering probably reflects a genetic tolerance to water deficits. The other clones, on the other hand, were less able to adjust their growth to match water supply and produced many larger leaves and so suffered more severely from infrequent watering. Consequently, clones 8038, 8049 and 8053 exhibited strong fluctuations in shoot

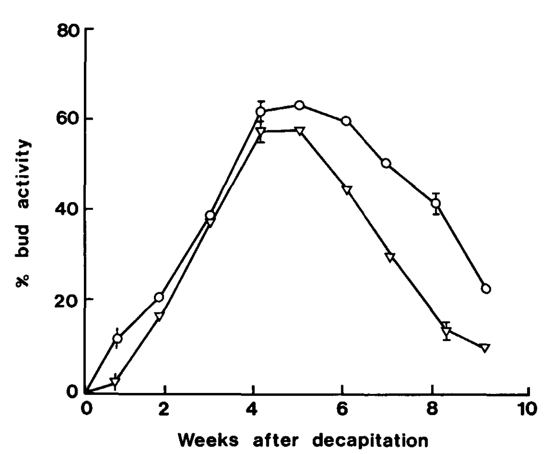

*Figure 6.* — Effects of daylength (▽ = 10 h, ○ = 19.5 h) on mean bud activity (percentage of buds growing more than 2mm week$^{-1}$) of decapitated plants of *T. scleroxylon*. Vertical bars = ± SE.

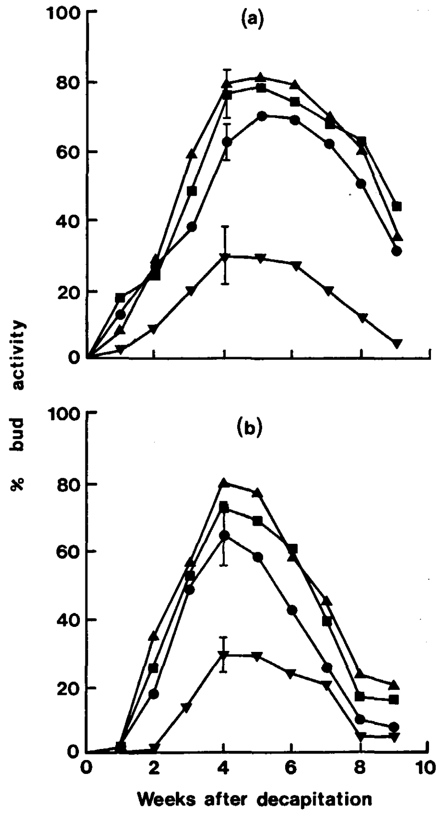

*Figure 7.* — Effects of daylength ((a) = 19.5 h, (b) = 10 h) on bud activity (percentage of buds growing more than 2 mm week$^{-1}$) of decapitated plants of 4 *T. scleroxylon* clones (▲ = 8038, ▼ = 8047, ■ = 8047, ● = 8053).

elongation and bud activity, depending on the stage of the watering cycle.

*Consistency of clonal responses*

In the previous study (LEAKEY and LONGMAN, 1986), it was not clear whether clones could be ranked for their responses to decapitation, although considerable uniformity in percentage bud activity under a range of treatments was found. It is apparent from the present study that while the absolute level of response of and clone to various treatments can change markedly, the relative response of one clone against another is much more consistent. Thus, for example, clone 8047 always had a significantly lower percentage bud activity than clone 8038 or 8049. These two clones responded similarly in six out of seven treatments. Likewise, clone 8053 was usually intermediate between 8047 and 8049. Inconsistencies did occur, however, in the relative responses of clones at high rates of fertilizer application and under the severest water stress.

The data from the three experiments presented here were subjected to correlation analysis, calculating the correlation coefficient, $r$, between bud activity of the clones under one treatment with that of the same clones under another treatment. In this test, a high value of r implies that the ranking of performance is insensitive to that treatment. Thus, comparing performance at two day-lengths, the correlation was 0.98 ($P = 0.01$), meaning that a good clone at short photoperiod was also a good clone at long photoperiod. However, in the fertilizer treatments the correlation was not significant, implying that the clones have a differential response to nutrient stress. For watering regime, there was some correlation: $r = 0.64$ when comparing daily with 12-day watering and $r = 0.75$ when comparing daily with 3-day watering.

The response of young plants to decapitation can be used as a fairly robust indicator of genetic variation in apical dominance as long as extreme environments are avoided, such as the 12-day watering cycle and the high rate of fertilizer application used in this study. Care must also be taken to maintain uniformity in the morphological and physiological state of the plants and in their growing environment. Of the morphological variables, the most important one to standardise seems to be leaf number, with 4, 5 or 6 leaves being optimal. Plant height and the position of decapitation seem to be less important, providing they are uniform throughout the batch. Suitable plants would seem to be those of about 20 nodes, decapitated to leave a fully expanded leaf at the uppermost node. A sthe application of this technique is aimed at the identification of clones with unusually strong apical dominance (*ie* low percentage bud activity), the growing conditions should be those conducive to maximising bud activity. Hence genetic screening should be applied under conditions of fairly high irradiance, nutrition and humidity, avoiding severe water stress.

The relationships between responses to decapitation and branching frequency as the basis for a "Predictive Test" for branching habit, will be presented elsewhere (LADIPO *et al.*, in prep. a and 1991).

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